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SOME NATURAL FACTORS LIMITING THE ABUNDANCE OF THE ALFALFA BUTTERFLY

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INTRODUCTION

THE EARLY HISTORY of the alfalfa butterfly as a pest is well covered in the works of Wildermuth (1911, 1914, 1920). In California and other parts of the West the caterpillar of this butterfly, *Colias eurytheme* Boisduval, is the most serious pest attacking alfalfa. Here, in cases of severe outbreaks, entire fields are often defoliated.

During the course of the alfalfa weevil investigation in the region adjacent to the San Francisco Bay and in the northwest portion of the San Joaquin Valley, it was observed that the amount of damage done by the alfalfa butterfly varied not only from year to year but from field to field. One of the reasons for this behavior came to light during September, 1938. In an alfalfa field near Tracy a large number of larvae were collected for use in toxicity studies. The alfalfa was about one third grown and supported a very large population of small larvae. At first it appeared that the developing population was sufficient to inflict serious damage. However, most of the larvae collected proved to be parasitized by a hymenopterous parasite, Apanteles flaviconchae Riley. Wildermuth (1914) probably referred to this parasite when he recorded A. flavicombe as a relatively unimportant parasite of the alfalfa butterfly at Salt Lake City, Utah. So effective was this parasite that on the next visit to the field the alfalfa butterfly larval population was greatly reduced, and the goldencolored cocoons of the parasite could be seen in large numbers attached to the

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^{*} See "Literature Cited" for complete citations which are referred to in the text by author

and date of publication.

⁵ Colias eurytheme is used here because it is the name by which the alfalfa butterfly is known in this country. Clark (1941), however, has changed the name to Colias chrysotheme (Esper). He stated that a comparison between eurytheme and the European and Asiatic chrysotheme showed no features by which the two may be differentiated. He listed the forms as follows:

Colias chrysotheme (Esper)

Colias chrysotheme eurytheme Boisduval Colias chrysotheme eriphyle W. H. Edwards Colias chrysotheme kootenai Cockle

Colias chrysotheme philodice Godart Colias chrysotheme guatemalana Staudingo

leaves of the alfalfa. The crop of alfalfa matured without any noticeable

injury being inflicted by the alfalfa butterfly.

Because of the spectacular nature of this control, it was thought advisable to investigate carefully the part Apanteles played in restricting the damage done by the host insect. For the past four years in a restricted area, the seasonal trends of the alfalfa butterfly population and parasitism by Apanteles have been followed, and are reported in this paper. In the course of this study numerous other insect parasites of the alfalfa butterfly were encountered. It is possible that several of these might serve as important natural checks, although preliminary observations indicate that none of these approached Apanteles in importance. It is hoped that it will be possible, in the future, to study them more thoroughly. Such an investigation would be very desirable to complete the picture. The main purpose of this paper is to discuss the natural enemies of the alfalfa butterfly which markedly affect the populations of this insect and which should be carefully considered in planning any control measures. A wilt disease which attacks the alfalfa butterfly is also discussed because of a relationship that appears to exist between this disease, the parasite (Apanteles flaviconchae Riley), and the alfalfa butterfly.

The area covered in this study embraces a region adjacent to the San Francisco Bay, and the west side of the lower San Joaquin Valley which includes the towns of Tracy, Vernalis, Westley, and Patterson. A striking difference was noted in alfalfa butterfly populations within these areas, which raises a question as to how far the findings of this study can be applied to other regions. Certainly caution should be used in comparing areas having markedly different climates.

However, a survey in 1942 of many of the alfalfa-producing sections in California revealed the parasite Apanteles flaviconchae to be present in all the areas visited. The parasite has been collected in the following counties: Alameda, Butte, Contra Costa, Fresno, Imperial, Kern, Kings, Los Angeles, Madera, Merced, Napa, Orange, Riverside, San Bernardino, San Diego, San Joaquin, Solano, Stanislaus, Tulare, Ventura, Yolo, and Yuba. In most of these the wilt disease has also been observed. It is the belief of the authors that these two important factors in the ecology of the alfalfa butterfly operate in the same manner as described in this paper throughout California.

EXPERIMENTAL METHODS USED

Populations of alfalfa butterfly larvae were determined by sweeping alfalfa fields in the areas studied. Usually at least 100 sweeps were made in each field, although fewer sweeps were sometimes made where extremely large populations were encountered. During the periods when the insect was most active, surveys were made at intervals of from 7 to 14 days, and the number of fields examined in the San Joaquin usually ranged between 10 and 15. In the region adjacent to San Francisco Bay the number of fields ranged from 4 to 8. Fields were seldom swept before the plants were one fourth grown, and an effort was made to select those fields representative of average conditions. The larvae

⁶ A No. 5 "Harrimac" collapsing, steel frame, landing net, manufactured by the Richardson Rod and Reel Company, Chicago, was used throughout this investigation. The frame is an ellipse, the major axis of which is 15 inches and the minor axis, 13 inches.

collected were segregated into two groups according to size. The "large" group contained all caterpillars which had advanced beyond the earliest part of the fourth instar, while all other larvae were considered "small."

The amount of parasitism by Apanteles was determined in the field. This was done by holding a larva between the thumb and forefinger. The head of the larva was pulled off with a forceps and enough pressure exerted on the larva to cause the parasite, if present, to be expelled. If the larva of the parasite is large, it spurts out; if small, it comes out usually adhering to the intestinal tract where it is easily seen. With a little practice, the examination can be made rapidly and accurately. It was not necessary to treat all larvae in the manner described above for, as the parasite develops, it distends the posterior end of the host (fig. 1) and can thus be detected. While Apanteles parasitizes the first three larval instars of the alfalfa butterfly, the first instar larvae were

never examined because of their very small size. In determining the number of small larvae parasitized, very late second, third, and early fourth instars were selected. These ranged from about 5 to 11 millimeters in length and were easiest to handle. The percentage of small larvae given as being parasitized was based on the number found to be parasitized in this size range. This method of determination was believed to give a very conservative estimate of the small larvae that were parasitized. At the size range indicated the parasites had developed to a size where they could more A readily be seen. It is possible that Apanteles may parasitize larvae of a size above the range indicated, but this seems to be rare. If oviposition had occurred recently in a larva, the egg or very young parasite would likely be overlooked. However,

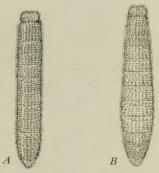


Fig. 1.—A, Normal alfalfa butterfly larva in early instar stage. B, Parasitized larva, showing swollen posterior end. (Both \times 5.)

since commonly 95 to 100 per cent of the larvae were found parasitized in counts made at progressive intervals, it would indicate that in most cases very few parasites are missed by the method of examination described above.

If the population in a field permitted, 100 larvae were examined for parasitism. In constructing graphs showing the percentage of parasitism, the figures used are based on the total number of parasitized and nonparasitized larvae of the size-range, as previously described, examined on any particular date.

The rearing dishes used for life-history studies were of the same type as used in the rearing of the garden centipede (Michelbacher, 1938). They were made by thoroughly mixing 10 parts of plaster of paris, 3 parts finely ground soil, and 1 part of animal charcoal. Water was added to the mixture and the whole stirred until the material had the consistency of rather thick cream. This was then poured into stender dishes to about the depth of ½ inch and allowed to set. These stender dishes, with their absorbent plaster, were found to be very well suited for rearing individual larvae and made accurate observations possible. The outside dimensions of the dishes used were: height, 30 millimeters and diameter, 50 millimeters. Fresh food was given to the caterpillars once a day during the first four instars, and twice a day during the fifth

instar. After pupation occurred the individuals were placed in pint Mason jars. To avoid spreading disease from one culture to another certain aseptic precautions were followed. Instruments were dipped in 10 per cent carbolic acid solution for at least 30 seconds, and the dishes were cleaned of feces with a camel's hair brush.

The temperature cabinets used in the investigation did not fluctuate more than \pm 1° F. The eggs used for life-history studies were obtained from butter-flies brought in from the field, and the parasites used were reared from parasitized alfalfa butterfly larvae collected in the field.

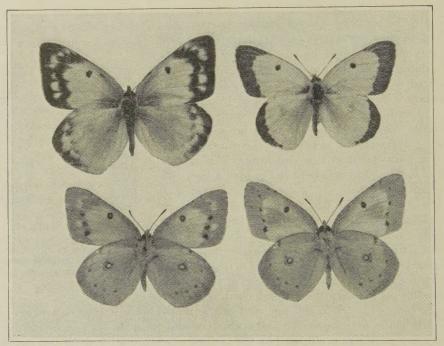


Fig. 2.—Adults of the alfalfa butterfly. Left, females; right, males; upper row, dorsal view; lower row, ventral view. (Natural size.)

LIFE HISTORY AND DEVELOPMENT OF THE ALFALFA BUTTERFLY

Everyone who has observed the alfalfa butterfly (fig. 2) in the field is struck by the rapidity of its development during the summer months. During this time, the broods appear about a month apart. The eggs (fig. 3), which are laid singly on the leaves of the alfalfa plants, are ribbed, and somewhat cigar-shaped. When first laid they are pearly white but as incubation continues they turn pinkish and, before hatching, the black head of the larva, which is apical in position, shows through the delicate eggshells. The hatching larva chews its way out, and frequently eats the whole shell before starting to feed on the leaves. The black head of the first instar larva distinguishes it from all other

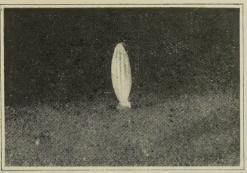


Fig. 3.—Egg of the alfalfa butterfly. (×15.)

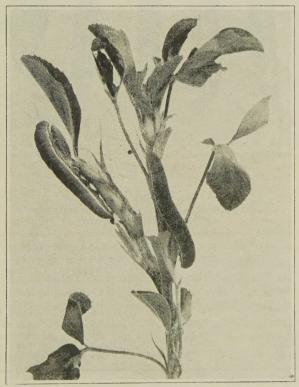


Fig. 4.—Mature larvae of the alfalfa butterfly as seen on alfalfa plants. (About natural size.)

stages. Before reaching maturity the larva casts its skin four times. The full-grown larva (fig. 4) is about 30 millimeters, or about $1\frac{1}{4}$ inches in length. It is of velvet-green color and along either side there is a white line with red markings. Down the back there may be two fine white lines (fig. 5, A). The length of the larvae in the different instars is shown in table 1. At first the larvae grow slowly and their feeding is not noticeable. However, by the time the fourth instar is reached considerable food is consumed and during the final

instar the larvae have a voracious appetite. Upon reaching maturity the larvae transform into light-green pupae (fig. 5, B) which are attached to the stubble and stems of the alfalfa. As the butterfly develops it can be seen within the pupal case and soon after this, it emerges. Most of the butterflies are yellow

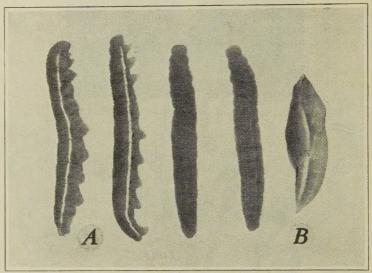


Fig. 5.—A, Four mature alfalfa butterfly larvae showing some differences in markings. B, Pupa. (All × 1.5.)

TABLE 1 LENGTH OF ALFALFA BUTTERFLY CATERPILLARS IN THE DIFFERENT INSTARS

Instar	Number	Length in millimeters			
	examined	Range	Mean		
Newly emerged	50	1.8-1.8	1.80		
First	22	1.8-3.0	*		
Second	21	3.0- 5.5	4.05 ± 0.17		
Third	21	4.5-8.0	6.31 ± 0.23		
Fourth	9	8.0-15.0	8.94 ± 0.51		
Fifth (early)	11	15.0-23.0	19.00 ± 0.87		
Fifth (late)		26.0-29.0	27.69 ± 0.29		

^{*} Data not available.

with black markings. The males can be distinguished from the females in that they have on the upper, outer surfaces of the wings a solid black border. The females are usually slightly larger and the black border is broken by yellow spots. The females also occur in a white color phase.

Some laboratory studies were conducted on the rate of development and duration of the various stages at constant temperatures of 80° and 90° F. The results of these studies are given in table 2. The time necessary for the butterfly to complete its life cycle from egg to adult at 80° F was approximately 21 days; and at 90°, about 17 days. The mean temperature in the portion of the

San Joaquin Valley where most of this investigation was conducted does not reach 80°, although over part of the area a mean temperature of close to 75° exists for a period of a month or two.

Although the present authors are aware that these data were obtained at constant temperatures and that the butterfly exists under highly fluctuating temperatures, they feel justified in stating that the alfalfa butterfly can easily complete its life cycle in a month during the summer; furthermore all the field observations indicate that during midsummer the life cycle is completed in 30 days or less. Although evidence in the literature is very scanty, it indicates that fluctuating temperatures may even accelerate development (Imms, 1937).

According to Wildermuth (1920) the alfalfa butterfly passes the winter in the pupal stage, although he stated that in the Southwest both larvae and

 ${\bf TABLE~2} \\ {\bf Rate~of~Development~of~the~Alfalfa~Butterfly~at~Constant~Temperatures} \\$

Stage	Number of indi-	Days at 80° F		Number	Days at 90° F	
	viduals	Range	Mean	of indi- viduals	Range	Mean
Egg	20	3-3	3 ± 0.01	24	2-3	2.5
First instar	38	2-3	2.6 ± 0.08	33	0.5-3	2.1 ± 0.12
Second instar	33	1-3	2.2 ± 0.06	41	1-3	1.8 ± 0.10
Third instar	25	1-3	1.8 ± 0.13	31	1-3	1.7 ± 0.11
Fourth instar	14	2-3	2.3 ± 0.12	22	1-3	2.1 ± 0.09
Fifth instar	6	4-5	4.3 ± 0.21	10	2-4	2.9 ± 0.18
Pupa	5	5–5	5 ± 0.01	8	4-5	4.1 ± 0.13
Total (hatch to emergence).			18.2	••		14.7
Total (time egg laid to		•••	21.2	••		17.2

adults could be taken every month in the winter. In the present investigation no thorough study has been made to determine how the insect passes the winter. In mild winters larvae can be collected during any month. They have not been collected in abundance, but when a search was made a few at least could be found. Adult butterflies are not seen to any extent until about the first of April. In cold winters, particularly, the insect probably passes the coldest period in the pupal stage, although it is possible that the adult may pass the winter in well-protected secluded places. Under any conditions, the winter and spring activity of the alfalfa butterfly is not great, and it is never found in abundance at that time. Shortly after the first of June, however, there is a rise in the larval population. Although not very noticeable it probably marks the first summer brood. There is a second much larger brood in July, and a still larger one during the end of August and the first part of September. Following this very large brood, there is a smaller one. The first severe attack by the pest occurs on the fourth and fifth crops. The seasonal trend of the larval population in the San Joaquin Valley for 1939-1942 inclusive are shown in figures 6 to 9. In the summer and fall there are four more or less distinct broods.

The seasonal trend of the larval population in the agricultural region adjacent to San Francisco Bay is very different from that in the northwest portion

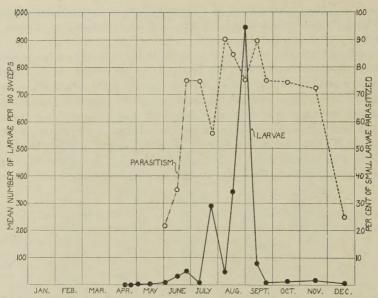


Fig. 6.—Alfalfa butterfly larval population and the per cent of the small larvae parasitized by *Apanteles flaviconchae*, in the northwest portion of the San Joaquin Valley, 1939. The part of the parasitism curve representing June is shown by dot and dash, since the percentage of parasitism was only estimated.

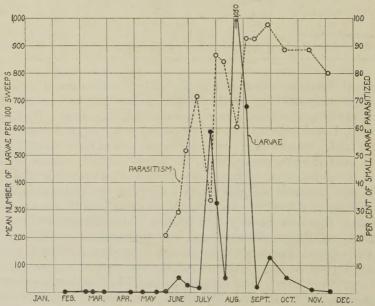


Fig. 7.—Alfalfa butterfly larval population and the per cent of small larvae parasitized by Apanteles flaviconchae, in the northwest portion of the San Joaquin Valley, 1940.

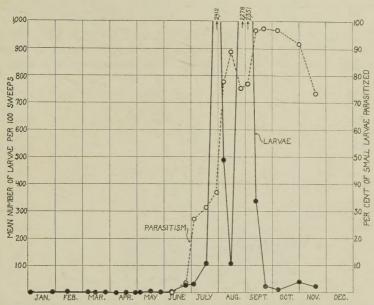


Fig. 8.—Alfalfa butterfly larval population and the per cent of small larvae parasitized by Apanteles flaviconchae, in the northwest portion of the San Joaquin Valley, 1941.

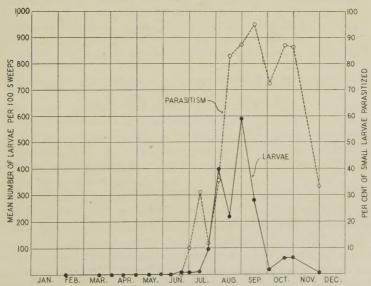


Fig. 9.—Alfalfa butterfly larval population and the per cent of small larvae parasitized by Apanteles flaviconchae, in the northwest portion of the San Joaquin Valley, 1942.

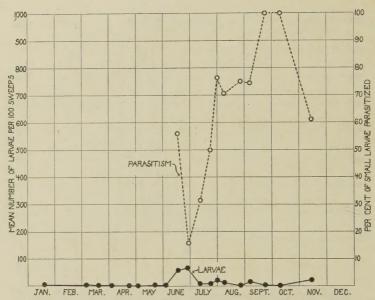


Fig. 10.—Alfalfa butterfly larval population and per cent of small larvae parasitized by Apanteles flaviconchae, in the agricultural region adjacent to San Francisco Bay, 1940.

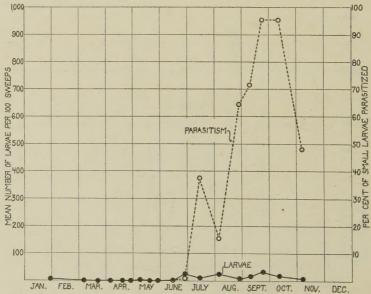


Fig. 11.—Alfalfa butterfly larval population and per cent of the small larvae parasitized by Apanteles flaviconchae, in the agricultural region adjacent to San Francisco Bay, 1941.

of the San Joaquin Valley. The winter activity is much the same but a wide departure occurs in summer activity. There is no marked build-up such as occurs in the San Joaquin Valley. Some factor, possibly associated with climate, is effective in limiting the numbers of alfalfa butterflies in the more coastal areas. The seasonal trends for 1940 and 1941 are shown in figures 10 and 11.



Fig. 12.—Adult Apanteles flaviconchae. (×17.)

LIFE HISTORY AND DEVELOPMENT OF APANTELES FLAVICONCHAE

Apanteles flaviconchae (fig. 12) is a hymenopterous parasite of the alfalfa butterfly larva. It completes its development (fig. 13) in a relatively short period and issues from the host larvae long before they have completed their growth. Soon after emerging, it spins a golden-colored or yellowish silken cocoon from which the adult emerges.

These cocoons are not gregarious as has been reported by Muesebeck (1921) and Viereck (1916), but are usually spun singly on the upper surface of an alfalfa leaf. One would suspect that the apparent gregariousness reported earlier was due probably to an unnatural method of rearing.

The time necessary for Apanteles to complete its development at a constant temperature of 80° F, was investigated. The information obtained is summarized in table 3. The time to complete the life cycle ranged from 11 to 13 days and depended upon the stage of the host parasitized. This study has shown that Apanteles is able to complete its life cycle in much less time than the alfalfa butterfly, and since it also is apparently able to find its host with ease, it has a combination of characters which make it a formidable factor in checking the damage done by the alfalfa butterfly.

Effect of Apanteles upon the Host.—Apparently only the early instars of the alfalfa butterfly are attacked by Apanteles. No difficulty was encountered in parasitizing the larvae in the laboratory. The parasites oviposit freely in any of the first three instars. In the field it is possible that the first- and second-instar larvae are more heavily parasitized. A host larva casts its skin twice after being parasitized in the first or second instar; and only once if it is parasitized in the third instar. Further development of the host is arrested, and the parasite completes its development and emerges. Thus the instar stage from which the parasite emerges is prolonged. It was noted that Apanteles emerged from host larvae of the third and fourth instars. That is certainly the usual

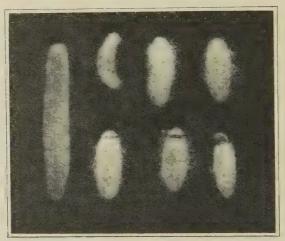


Fig. 13.—Stages in the development of Apanteles flaviconchae. Left, host caterpillar from which the parasite is about ready to emerge. The upper row shows at the left a mature parasite larva, and at the right two cocons of the parasite. The lower row shows three cocons from which the parasite has emerged. (×5.)

condition, although Floyd (1940) reported rearing the parasite from fifthinstar larvae and made no mention of rearing it from any of the earlier instars.

The length of time necessary for the parasite to complete its life history is increased if oviposition occurs in larvae of the first instar; this is probably because of the very small size of the host larva at the time of oviposition. Apparently the available food is so limited that more time is needed than when later instars are parasitized. The hosts were killed outright when the parasites emerged from larvae that were parasitized in the first or second instar. Where third-instar larvae were parasitized the hosts were thoroughly incapacitated but in some cases they remained alive for several days following the emergence of the parasite. Apanteles destroys its host before it has had opportunity to do much feeding; and, furthermore, it may parasitize nearly the whole larval population. These facts make Apanteles a very effective natural check on the alfalfa butterfly.

Apanteles will lay more than a single egg in a host larva. In the laboratory some evidence was obtained to indicate that a host might be killed by having

too many eggs deposited in it. It is very possible that this happens in the fields where the adult parasite population is large and the host population is small. Such behavior is not to the best advantage of the parasite, and may reduce its effectiveness.

Because Apanteles is a parasite of the alfalfa butterfly, its seasonal population trend is closely associated with that of its host. Apanteles has been taken every month of the year except January. In 1940 it was not taken until March 13, but in 1941 it was found rather easily on February 13, and in 1942 parasitized alfalfa butterfly larvae were taken on February 10. The way in which it passes the coldest part of the year has not been investigated but it probably survives the winter in the adult stage or in the cocoon. As in the case of its host, Apanteles does not exhibit a great deal of activity before the first of June. From this time on, the parasite becomes more abundant. The number of host

TABLE 3 TIME REQUIRED FOR THE DEVELOPMENT OF Apanteles at 80° F

Stage of host parasitized	Stage of host from which parasite emerged	Days in host	Days in cocoon stage	Total days from oviposition to emergence
First instar	Third instar	81/2	41/2	13
Second instar	Fourth instar	7	4	11
Third instar	Fourth instar	7	4	11

larvae parasitized varies considerably during the peak broods of the alfalfa butterfly, but at all times a large proportion of the smaller larvae are parasitized. Although there may be considerable variation in the degree of parasitism in early summer in different years, this difference is lost by late summer when nearly all the larvae are parasitized; and this high degree of parasitism continues into December.

The seasonal parasitism trends in the northwest portion of the San Joaquin Valley for the years 1939–1941, inclusive, are shown in figures 6 to 9, and for the region adjacent to the San Francisco Bay for the years 1940 and 1941, in figures 10 and 11. The trends are plotted only for the months of June through November. Although a number of parasitized larvae may be taken during the winter and spring, not a sufficient number could be collected on any particular survey to give a dependable figure. Even during the summer in the region adjacent to the San Francisco Bay, some of the percentages plotted were based on an examination of relatively few larvae.

EFFECTIVENESS OF PARASITISM BY APANTELES

The value of *Apanteles* in controlling the alfalfa butterfly can hardly be overestimated. It is one of the most important natural factors holding this serious pest in check. In certain fields and districts it has completely dominated the situation, and time and again it has saved the alfalfa crop from nearly complete destruction. The effectiveness of the parasite has not been so complete in some years as others. In 1939 not a single seriously infested alfalfa field was observed in a region that covered an area from west of Tracy to south of Vernalis. In this large area the greatest number of alfalfa butterfly larvae

collected per 100 sweeps never exceeded 220. Over most of this area the degree of parasitism of small larvae in any field during the summer seldom fell below 80 per cent. The completeness of parasitism is corroborated by the fact that very few large larvae were collected at any time in this region. The only heavy infestation of the alfalfa butterfly encountered in the northwest portion of the San Joaquin Valley in 1939 was in a small region near Westley. Here several fields were seriously damaged, although in the most heavily infested area there were some fields that were fully protected by *Apanteles*. For example, there was one field where 685 larvae were collected per 100 sweeps, all of them small, and 99 per cent were parasitized.

In 1940 the outbreak of the butterfly was more severe than in 1939. Scattered through most of the area there were fields that suffered serious injury. Even in the face of this attack *Apanteles* played a very important role in

reducing damage and many fields were completely protected.

The 1941 butterfly outbreak was the most serious observed since work on the investigation of alfalfa insects was started in 1933. In scattered fields the alfalfa was almost defoliated, and in others it was seriously attacked; nevertheless, *Apanteles* saved many fields from economic loss.

It is probable that the damage done by the alfalfa butterfly during the past four years represents the greatest fluctuation that might be expected to occur. The immediate question that arises is: why should there be such a wide range in the damage done from year to year? It may be that climate is partly responsible. Parasitism may also play a part, and in looking over the experimental data there is some evidence that strongly indicates that this is the case. If the amount of parasitism during June, in 1939, 1940, and 1941 is examined, it is noted as greatest in 1939, somewhat less in 1940, and considerably less in 1941. The trends for these three years are shown in figures 6 to 8 for the months of June through November. The figures plotted are the percentage of larvae parasitized, based upon the total number examined for parasites in all fields surveyed on any particular date. Information for June 1939 is indicated by dot-and-dash line, and represents an estimate, only because the data taken up to that time were general and not based on actual counts. It should be noted that the conditions which exist in individual fields or even districts, are lost when information is presented in the graphical form just mentioned. Fields having a high population exert more influence on a graph because of the larger number of larvae that are available for examination; in many fields only a few larvae could be collected and parasitism in such areas might be extremely high, but because of the small number of larvae available the importance of parasitism is not fully shown.

The early parasitism trend during the time that the first brood of alfalfa butterfly larvae is making its appearance may give some indication of the destructiveness of the later broods. In general, the greater the degree of parasitism in June, the less serious will be the attacks from the later broods. This is certainly indicated in figures 6, 7 and 8. The first brood is small and if parasitism is high at that time, it is possible that enough larvae will be destroyed so that the later broods will be much reduced. Further, a large population of adult parasites is produced early and these might play an important part in holding the larval butterfly population in check. During the early summer,

when the environmental resistance is apparently low, aside from cultural kill at the time of cutting, *Apanteles* appears to be the principal factor in the environmental resistance effective in reducing size of the brood. The wilt disease that becomes so important later in the summer apparently plays no part at this time. For this reason, if *Apanteles* is slow in starting, the amount of parasitism will be small during this critical period, and the stage is set for later serious infestations of the alfalfa butterfly.

Further evidence in support of this is shown in table 4 in which some relations existing between the alfalfa butterfly and *Apanteles* during the development of the first brood for the years 1939 to 1942, inclusive, are summarized. With the exception of 1942, the higher the degree of parasitism of small larvae the greater the proportion of parasites to each large caterpillar. This is important because it is the large caterpillars that have escaped parasitism, that give rise to the later broods of butterflies. Thus the more parasites per

TABLE 4 Parasitism by Apanteles in the First Brood of the Alfalfa Butterfly Larvae in the Years 1939-1942

Year		Average number of parasitized larvae per field (100 sweeps)	Per cent of parasitized larvae	Average number of large larvae per field (100 sweeps)	Number of parasites per large larva
1939	8.40	4.30	51.20	0.71	6.10
	13.10	4.90	37.40	18.00	0.27
	7.00	1.00	14.30	14.00	0.07
	3.10	0.30	9.70	4.70	0.06

caterpillar the greater the environmental resistance will be on the following broods. In 1939 this relation was 6.1 parasites to each large larva while in 1941 it was 0.07 to each large larva. In the former year very little damage was done by the succeeding butterfly broods, while in the latter year severe damage occurred. In 1940 some damage occurred and, although much less than in 1941, it was considerably more than in 1939. The weather in the late spring and early summer of 1942 was cool. There was a marked departure from the normal, and the weather conditions were somewhat similar to those which normally occur nearer the coast, a climatic region where damage by the alfalfa butterfly has never been observed by the authors. The cooler weather conditions probably account for the small first brood. Despite the low parasitism, the ratio of parasites to large alfalfa caterpillars was 0.06 to 1.0, the lack of damage in 1942 can be attributed to the small first brood. It is only in such cases where parasitism is negligible that the size of the brood is important in determining the destructiveness of later populations.

The percentage of parasitism during the first brood and its relation to the size of the later broods is a very complicated matter. First, the amount of parasitism is affected by the size of the fall population of *Apanteles* and *Colias*, the winter mortality, and various climatic and other unknown factors during spring and early summer. Moreover, the effect of the parasite may be modified by cutting and other cultural practices, by the wilt disease, and the climate prevailing for the season. In spite of this we feel that the amount of parasitism in the first brood is indicative of later infestations, especially when taken in

consideration with the amount of large larvae in that brood. In the four years that we have studied these insects, in only one field where the parasitism of small larvae was over 35 per cent of the first brood did serious infestations develop later; and in that case the first brood produced an unusually high percentage of large worms.

The data on the first brood of alfalfa butterfly gives an excellent field illustration of the effect of host density on parasitism. Where host density is low, correspondingly small parasite populations occur; but where the population density of small larvae is high many parasites complete their development.

This is indicated in the following tabulation:

Small larvae per 100 sweeps	8		Parasites produced
0			0.00
1			0.15
2.			0.36
3			0.50
4-10			1.33
11-15			2.59
16-25			4.55
26-75			11.80
76+		,	32.90

These results probably can be explained by the difficulty the parasite has in finding its host when the population density is low.

If for some reason *Apanteles* is not able to check the later broods of the alfalfa butterfly effectively, the wilt disease will enter the picture. Therefore, the wilt disease becomes more evident when *Apanteles* is less effective. For this reason wilt disease played a more important role in 1941 than in the previous years. However, it appears to be present at all times and reduces larval populations which have escaped other natural enemies.

In order to show the part Apanteles played in limiting damage of the alfalfa butterfly, tables 5 to 7 are included. These tables give the alfalfa butterfly larval population trends and the percentage of parasitism of small larvae by Apanteles during the development of the midsummer infestation of the alfalfa butterfly in the northwest portion of the San Joaquin Valley for the years 1939, 1940, and 1941, in individual fields. In 1939 the larvae were not segregated into large and small larvae, and for that year only the total number of larvae collected is given. From these tables it is seen that in many cases Apanteles was very effective in reducing the alfalfa butterfly population. For instance, on September 3, 1940, in one field near Tracy, 2,180 larvae were collected per 100 sweeps. Of this number, 330 were large; and of the 1,850 small ones, 99 per cent were parasitized. On September 3, 1941, in one field near Westley, 2,884 larvae were collected per 100 sweeps. Of these, 720 were large, and 91 per cent of the 2,164 small ones were parasitized. This same condition also existed in all the surrounding fields. The populations would have been much greater if it had not been for Apanteles. Parasitized larvae are killed before they reach maturity; consequently many are removed as compared with a field where the effects of the parasite are absent.

In this study it has been observed that the number of butterfly adults noted is little indication of how much damage will be done by the pest. If the envi-

TABLE 5

Alfalfa Butterfly Larval Populations and Parasitism by Apanteles During the Midsummer Infestation in the Northwest Portion of the San Joaquin Valley, in 1939

SAN JOAQUIN VALLEY, IN 1939		
Location of field	Total larvae, per 100 sweeps	Per cent of small larvae parasitized
July 10		
Tracy 1 mile east of Tracy. 4 miles south of Tracy 2 miles north of Vernalis 2 miles south of Westley. Patterson. Patterson.	10 8 12 10 7 2 3	79 38 82 13 85 100
July 24		
5 miles north of Tracy. 5 miles north of Tracy. 1 mile east of Tracy. 1 mile east of Tracy. 6 miles south of Tracy. 2 miles south of Westley. 2 miles south of Westley. 2 miles south of Westley. 2 miles north of Patterson	82 158 25 50 60 127 778 129 65	67 27 90 94 82 72 22 13 91
August 7		
5 miles north of Tracy. 1 mile east of Tracy. 1 mile east of Tracy. 5 miles south of Tracy. 2 miles south of Westley. Patterson	10 10 30 103 121 10	80 88 95 92
August 16		
Tracy 1 mile east of Tracy. 1 mile east of Tracy. 6 miles south of Tracy. 4 miles north of Vernalis. 2 miles south of Westley. 2 miles south of Westley.	2 2 2 10 2 675 1,710	100 100 100 98 70

TABLE 5 (Continued)

Location of field	Total larvae, per 100 sweeps	Per cent of small larvae parasitized
August 31		
5 miles north of Tracy. 5 miles north of Tracy. 1 mile east of Tracy. 6 miles south of Tracy. 4 miles north of Vernalis. 2 miles south of Vernalis. 2 miles north of Westley. Westley. 2 miles south of Westley. 2 miles south of Westley. 2 miles south of Westley. 2 miles north of Patterson.	175 170 171 210 10 160 620 3,236 3,560 1,822 275	53 93 94 95 87 50 7 60
September 11		
Tracy 1 mile east of Tracy 6 miles south of Tracy 2 miles south of Vernalis 2 miles south of Westley	2 68 2 116 685	100 79 88 99
September 22		
1 mile east of Tracy. 6 miles south of Tracy. 6 miles south of Tracy. 4 miles north of Vernalis. Westley. 2 miles south of Westley. 2 miles south of Westley.	1 2 4 2 12 50 2	

TABLE 6

Alfalfa Butterfly Larval Populations and Parasitism by Apanteles During the Midsummer Infestation in the Northwest Portion of the San Joaquin Valley, in 1940

SAN JOAQUIN VAL	LEY, IN 194	.0		
Location of field	Total larvae per 100 sweeps	Large larvae per 100 sweeps	Small larvae per 100 sweeps	Per cent of small larvae parasitized
July 9		·	·	
Tracy	42	.7	35	75
Tracy	5	0	5	100
6 miles south of Tracy	24	0	24	-
5 miles south of Tracy	0	0	0	
3 miles south of Tracy	3	0	3	100
7 miles south of Tracy	21	2	19	78
4 miles north of Vernalis	0	0	0	
1 mile south of Vernalis	2	1	1	
2 miles south of Vernalis	18	1	17	12
Westley	4	0	4	100
2 miles north of Patterson	77	4	73	78
1 mile north of Patterson	0	0	0	
Patterson	18	0	18	100
July 22			<u>' </u>	
Tracy	89	71	18	25
Tracy	375	186	189	50
4 miles south of Tracy	232	1	231	28
6 miles south of Tracy	814	426	388	16
5 miles south of Tracy	2,134			
Vernalis	42	2	40	25
2 miles south of Vernalis	43	23	20	25
2 miles south of Westley	645	430	215	16
2 miles south of Westley	900			
Patterson	1	1	0	1
July 30		1		
		1		100
Tracy	5	2	3	100
Tracy	111	61	50	94
Tracy	160	63	97	89 95
3 miles south of Tracy	83	21	62	95 86
4 miles south of Tracy	387	203	184	25
6 miles south of Tracy	804			
5 miles south of Tracy	2,016 40	4	36	100
Vernalis.		81	107	87
2 miles south of Vernalis.	188 318	300	107	50
2 miles south of Westley	318 121	300	10	00
2 miles south of Westley	25	7	18	93
2 miles north of Patterson	1	1	0	
1 accersori	1			

TABLE 6 (Continued)

Location of field	Total larvae per 100 sweeps	Large larvae per 100 sweeps	Small larvae per 100 sweeps	Per cent of small larvae parasitized
August 8				
Tracy	18	0	18	92
3 miles south of Tracy	7	1	6	100
4 miles south of Tracy	42	12	30	93
5 miles south of Tracy	16	0	16	100
5 miles south of Tracy	255	195	60	50
6 miles south of Tracy	35	0	35	95
4 miles north of Vernalis	11	0	11	. 100
Vernalis	7	3	4	66
Westley	240	2	238	96
Westley	11	1	10	85
2 miles south of Westley	6	0	6	100
2 miles south of Westley	14	6	8	83
August 23		-		
Tracy	1,341	550	791	78
4 miles south of Tracy.	148	14	134	92
5 miles south of Tracy	325	0	325	83
6 miles south of Tracy.	600	18	582	90
1 mile south of Vernalis.	400	200	200	80
2 miles south of Vernalis.	690	165	525	42
		1		i
2 miles south of Westley	798	2	1 796	70
2 miles south of Westley	798 6,300	4,000	796	70
2 miles south of Westley. 2 miles south of Westley. 2 miles north of Patterson.		1		1
2 miles south of Westley	6,300	4,000	2,300	40
2 miles south of Westley	6,300 42 864	4,000	2,300 42	40
2 miles south of Westley	6,300 42 864	4.000	2,300 42 414	50
2 miles south of Westley	6,300 42 864 3	4.000 0 450	2,300 42 414	50
2 miles south of Westley	8,300 42 864 3 315 2,180	4,000 0 450 7 330	2,300 42 414 308 1,850	99 99
2 miles south of Westley	6,300 42 864 3	4.000 0 450	2,300 42 414	50
2 miles south of Westley. 2 miles north of Patterson. Patterson. September Tracy. Tracy. 4 miles south of Tracy. 5 miles soutn of Tracy.	6,300 42 864 3 3 315 2,180 307	4.000 0 450	2,300 42 414 308 1,850 306	99 99 99 94
2 miles south of Westley. 2 miles north of Patterson. Patterson. September Tracy. 4 miles south of Tracy. 5 miles south of Tracy. 5 miles south of Tracy.	6,300 42 864 3 3 315 2,180 307 1,830	7 330 1 780	2,300 42 414 308 1,850 306 1,050	99 99 99 94 69
2 miles south of Westley. 2 miles north of Patterson. Patterson. September Tracy. Tracy. 4 miles south of Tracy. 5 miles south of Tracy. 5 miles south of Tracy. 2 miles south of Tracy. 2 miles south of Tracy. Vernalis. 2 miles south of Vernalis.	6,300 42 864 3 3 315 2,180 307 1,830 1,200	4,000 0 450 7 330 1 780 100	2,300 42 414 308 1,850 306 1,050 1,100	99 99 99 94 69 88
2 miles south of Westley. 2 miles north of Patterson. Patterson. September Tracy. Tracy. 4 miles south of Tracy. 5 miles south of Tracy. 5 miles south of Tracy. 2 miles south of Vernalis. 2 miles south of Vernalis.	6,300 42 864 3 3 315 2,150 307 1,830 1,200 17	7 330 1 780 100 0	2,300 42 414 308 1,850 306 1,050 1,100 17	99 99 99 94 69 88
2 miles south of Westley. 2 miles north of Patterson. Patterson. September Tracy. 4 miles south of Tracy. 5 miles south of Tracy. Vernalis. 2 miles south of Vernalis. 2 miles south of Vernalis. 2 miles south of Vernalis.	3 315 2,180 307 1,200 17 540	7 330 1 780 100 0 306	2,300 42 414 308 1,850 306 1,050 1,100 17 234	99 99 99 94 69 88 100 92
2 miles south of Westley. 2 miles north of Patterson. Patterson. September Tracy. 4 miles south of Tracy. 5 miles south of Tracy. Vernalis. 2 miles south of Vernalis. 2 miles south of Vernalis. 2 miles south of Vernalis.	6,300 42 864 3 3 315 2,180 307 1,830 1,200 17 540 533	7 330 1 780 100 0 306 65	2,300 42 414 308 1,850 306 1,050 1,100 17 234 468	99 99 99 94 69 88 100 92 97
2 miles south of Westley	6,300 42 864 3 3 2,180 307 1,830 1,200 17 540 533 287	7 330 1 780 100 0 306 65 1	2,300 42 414 308 1,850 306 1,050 1,100 17 234 468 286	99 99 94 69 88 100 92 97
2 miles south of Westley. 2 miles north of Patterson. Patterson. September Tracy. 4 miles south of Tracy. 5 miles south of Tracy. Vernalis. 2 miles south of Patterson.	6,300 42 864 3 3 315 2,180 307 1,830 1,200 17 540 533 287 151 86	7 330 1 780 100 0 306 65 1 6	2,300 42 414 308 1,850 306 1,050 1,100 17 234 468 286 145	99 99 94 69 88 100 92 97 100 97
2 miles south of Westley. 2 miles north of Patterson. Patterson. September Tracy. 4 miles south of Tracy. 5 miles south of Tracy. 5 miles south of Tracy. 2 miles south of Vernalis. 2 miles north of Patterson. Patterson. September	6,300 42 864 3 3 2,180 307 1,830 1,200 17 540 533 287 151 86	7 330 1 780 100 0 306 65 1 6 12	2,300 42 414 308 1,850 306 1,050 1,100 17 234 468 286 145 74	99 99 99 94 69 88 100 92 97 100 97
2 miles south of Westley. 2 miles north of Patterson. Patterson. September Tracy. 4 miles south of Tracy. 5 miles south of Tracy. 5 miles south of Tracy. 2 miles south of Vernalis. 2 miles south of Vernalis. 2 miles south of Vernalis. 2 miles south of Patterson. Patterson. September	6,300 42 864 3 3 315 2,180 307 1,830 1,200 17 540 533 227 151 86	4,000 0 450 7 330 1 780 100 0 306 65 1 6 12	2,300 42 414 308 1,850 306 1,050 1,100 17 234 468 286 145 74	99 99 99 94 69 88 100 92 97 100 97 94
2 miles south of Westley. 2 miles north of Patterson. Patterson. September Tracy. 4 miles south of Tracy. 5 miles south of Tracy. 2 miles south of Vernalis. 2 miles south of Vernalis. 2 miles south of Patterson. Patterson. September	6,300 42 864 3 3 315 2,180 307 1,830 1,200 17 540 533 287 151 86	7 330 1 780 100 0 306 65 1 6 12	2,300 42 414 308 1,850 306 1,050 1,100 17 234 468 286 145 74	99 99 99 94 69 88 100 92 97 100 97 94
2 miles south of Westley. 2 miles north of Patterson. Patterson. September Tracy. Tracy. 4 miles south of Tracy. 5 miles south of Tracy. 2 miles south of Vernalis. 2 miles south of Vernalis. 2 miles south of Patterson. Patterson. September September	6,300 42 864 3 3 315 2,180 307 1,830 1,200 17 540 533 287 151 86	7 330 1 780 100 0 306 65 1 1 6 12	2,300 42 414 308 1,850 306 1,050 1,100 17 234 468 286 145 74	99 99 99 94 69 88 100 92 97 100 97 94
2 miles south of Westley. 2 miles north of Patterson. Patterson. September Tracy. Tracy. 4 miles south of Tracy. 5 miles south of Tracy. Vernalis. 2 miles south of Vernalis. 2 miles south of Vernalis. 2 miles south of Vernalis. 2 miles north of Patterson. Patterson.	6,300 42 864 3 3 315 2,180 307 1,830 1,200 17 540 533 287 151 86	7 330 1 780 100 0 306 65 1 6 12	2,300 42 414 308 1,850 306 1,050 1,100 17 234 468 286 145 74	99 99 94 69 88 100 92 97 100 97 94

TABLE 7

Alfalfa Butterfly Larval Populations and Parasitism by Apanteles During the Midsummer Infestation in the Northwest Portion of the San Joaquin Valley, in 1941

Location of field	Total larvae per 100 sweeps	Large larvae per 100 sweeps	Small larvae per 100 sweeps	Per cent of small larvae parasitized
July 17				
1 mile east of Tracy. 1 mile east of Tracy. 4 miles south of Tracy. 5 miles south of Tracy. 6 miles south of Tracy.	77 132 11 1	22 66 4 0	55 66 7 1	43 10 50 100
Vernalis	95 82 1 564	44 57 0 268	51 25 1 296	52 40
July 29				_,
3 miles south of Tracy. 3 miles south of Tracy. 5 miles south of Tracy. 6 miles south of Tracy. 8 miles southwest of Tracy. Vernalis. 2 miles south of Vernalis.	920 706 1,750 736 13,800 80 460	780 392 1,630 662	140 314 120 74	50 48 12 64 47
2 miles south of Westley	1,474 1,784	402 1,576	1,072 208	15 35
1 mile east of Tracy. 3 miles south of Tracy. 4 miles south of Tracy. 5 miles south of Tracy. 5 miles south of Tracy. 6 miles south of Tracy. 1 mile south of Vernalis. 2 miles south of Vernalis. 2 miles south of Vernalis 2 miles south of Patterson. Patterson. 2 miles east of Patterson.	12 258 139 105 172 738 410 124 1,930 2,036 185 258	0 194 1 4 148 610 302 90 1,360 1,812 80 160	12 64 138 101 24 128 108 34 570 224 105 98	100 84 92 84 50 73 53 88 72 48 88
August 1	4	1	i	1
3 miles west of Tracy 2 miles west of Tracy 1 mile east of Tracy 1 mile east of Tracy 3 miles south of Tracy 3 miles south of Tracy 5 miles south of Tracy 6 miles south of Tracy 2 miles south of Tracy 2 miles south of Vernalis Westley 3 miles north of Patterson 3 miles north of Patterson	61 104 133 43 101 172 83 80 50 264 182 76 258	21 2 1 1 38 3 5 3 3 0 11 22 43 230	40 102 132 42 63 169 78 77 20 253 160 33 28	94 93 98 100 85 99 96 97 100 83 79 71
2 miles north of Patterson	129 33 68	9 7	24 61	100

TABLE 7 (Continued)

TABLE 7 (CO				
Location of field	Total larvae per 100 sweeps	Large larvae per 100 sweeps	Small larvae per 100 sweeps	Per cent of small larvae parasitized
August 2	6			
Tracy.	1.374	16	1.358	88
1 mile east of Tracy	527	42	485	84
3 miles south of Tracy.	547	110	437	67
4 miles south of Tracy	2,086	484	1,602	64
6 miles south of Tracy	3,208	1,454	1,754	67
2 miles south of Vernalis	870	50	820	64
Westlev	11,336	5,064	6,272	42
2 miles south of Westley	874	4	870	97
3 miles northwest of Patterson	2,284	516	1,768	42
Patterson	1,240	92	1,148	90
Septembe	r 3	1	L	-1
		1		
Tracy	1,032	136	896	96
3 miles south of Tracy	9,100	1.		1 ::
3 miles south of Tracy	2,268	1,068	1,200	64
4 miles south of Tracy	378	. 6	372	90
4 miles south of Tracy	4,564	1,888	2,676	82
5 miles south of Tracy	2,238	700	1,538	16
6 miles south of Tracy	2,256	1,296	960	86
Vernalis	331	84	247	62
2 miles south of Vernalis	1,296	1,140	156	64
2 miles south of Westley	2,884	720	2,164	91
2 miles south of Westley	2,320	376	1,944	88
2 miles northwest of Patterson	1,520	494	1,026	76
Patterson	376	16	360	96
Septembe	r 12			-
4 miles northwest of Tracy	167	39	128	96
Tracy	265	2	263	99
3 miles south of Tracy	583	14	569	98
4 miles south of Tracy	28	0	28	100
5 miles south of Tracy	71	0	71	100
5 miles south of Tracy	1,292	736	556	84
6 miles south of Tracy	75	1	74	96
Vernalis	540	46	494	98
2 miles south of Vernalis.	480	70	410	95
	144	17	127	94
		1 41	121	1
2 miles south of Westley		2	250	1 00
2 miles south of Westley	261	2	259	99
2 miles south of Westley	261 2	0	2	100
	261	_		

ronmental resistance is low, an almost unnoticed population of butterflies will give rise to destructive larval populations. If the environmental resistance is high, large numbers of butterflies may not be able to produce enough larvae to do any damage. At times butterflies have been so abundant that stubble fields have appeared as if they were actually moving. In spite of such large populations at the start of a new crop, little damage has been done in certain localities, largely because of *Apanteles*, and the action of the wilt disease.

The factors that make *Apanteles* a very effective parasite are as follows: (1) it has a shorter life cycle than its host; (2) it apparently finds its host with ease; and (3) it destroys its host before it has had an opportunity to do any

appreciable damage.

EFFECT OF THE WILT DISEASE ON THE ALFALFA BUTTERFLY

The importance of the wilt disease in checking the ravages of the alfalfa butterfly has been observed by Wildermuth (1911, 1914, 1916, 1920), Cartwright and associates (1933), and at the Kansas station (1924). Whether the causal agent is a bacterium or a virus is not definitely known. However, Brown (1930) describes a disease of lepidopterous larvae which attacks the alfalfa butterfly and claims the causal organism to be Staphylococcus flaccidifex (Glaser). It is not known if this disease is the same as that which occurs in California. Most available information would indicate that it is bacterial in nature. The disease caused the death of the larvae in a very short time. Diseased larvae can usually be first detected when the color turns from the normal green to a paler yellowish or grayish green. Shortly after this stage is reached the caterpillars die, turn dark in color, and wilt down to a watery, decaying mass. The dead caterpillars usually remain clinging to the alfalfa stems and often, where the disease has attacked large populations, the dead caterpillars may be seen hanging from the alfalfa by the thousands. From observations made in the laboratory it appears that once a larva is infected with the disease, its further development may be arrested. It was almost a certain sign that the disease is developing when larvae, being reared under constant temperatures, failed to molt as expected. It is also possible that larvae unusually resistant

⁷ A few experiments designed to identify the etiological agent responsible for the disease were carried out by the junior author together with Dr. Michael Doudoroff of the Department of Bacteriology. A gram-positive yellow diplococcus, possibly identical with Staphylococcus (?) flaccidifex (Glaser) was found present in the intestinal contents and tissues of dying and dead larvae with remarkable regularity, but not universally. When present, it was practically the only organism that could be cultured. However, no bacteria could be isolated from several larvae which had died with similar symptoms, and in two cases only a colorless facultative catalase-negative diplococcus (probably a lactic acid bacterium) was found. Furthermore, the yellow diplococcus was found on several occasions in feces of apparently healthy larvae which later emerged successfully as butterflies, although the intestinal contents of such normal larvae did not show the presence of the organisms to any extent. Fresh feces were also relatively lacking in bacterial flora, indicating a later development of the bacteria. Attempts to infect larvae raised from eggs with pure cultures of the diplococcus by feeding and injection gave no significant results, since a large number of control individuals died of the same or similar disease, and the relative number of survivors were approximately the same for treated and untreated caterpillars. From these observations, it seems likely that the yellow coccus is not the primary causal agent, although the inability to raise healthy larvae made carefully controlled experiments impossible. It would seem that another cause, possibly a virus, must be considered in the etiological studies. Chapman and Glaser (1915) suggested that such a virus might be the causal agent.

may harbor the disease without showing it externally. This may account for the fact that the disease is sometimes carried over into the pupa and the latter

stage killed by it.

The disease is beyond doubt one of the most important of the natural checks upon the alfalfa butterfly. Usually two conditions, high humidity and a large host population, are needed before the disease reaches epidemic proportions. Certainly where a destructive population of alfalfa butterfly larvae is developing, a timely irrigation may make the environment very favorable for the development of the disease. Other investigators who mention moisture as favoring the disease are Wildermuth (1911, 1914, 1916, 1920), Cartwright and associates (1933), and the Kansas Agricultural Experiment Station (1924).

In many cases the beneficial action of the disease does not come into play until the alfalfa crop is seriously damaged. In some instances nearly complete defoliation may occur before feeding is checked. However, once started under favorable conditions the disease can destroy the caterpillar population in a remarkably short period. The following will illustrate this. On July 29 in one field there were approximately 14,000 larvae collected per 100 sweeps. At this time the wilt disease was just beginning to appear. Three days later hundreds of thousands of dead worms were observed clinging to the alfalfa, and only 40 live caterpillars were collected per 100 sweeps. Many of these were infected and on August 6, only 13 larvae were collected per 100 sweeps. Most of these had the early symptoms of the disease.

The disease does not always reach epidemic proportions. Cases have been observed where the disease continues to kill enough caterpillars so that the alfalfa can grow and produce a commercial crop. Where this occurs, caterpillars and disease can be found during the entire growth of the crop and, while some damage may be done, the disease saves the crop from total destruction.

The wilt disease gains in importance as the larval population increases. It apparently does not attack the brood of caterpillars that makes its appearance in June, being largely restricted to the midsummer and late summer broods. It becomes the most important natural factor checking the alfalfa butterfly larval population in fields where *Apanteles* is unable to hold the caterpillars in check.

THE EFFECT OF THE WILT DISEASE ON APANTELES

From observations in the field it would seem that sometimes the wilt disease has an adverse effect upon Apanteles. This appears to be particularly true where the disease is present in epidemic proportions. However, cases have been noted where Apanteles has dominated the situation after the wilt disease had first reduced the number of larvae; where this occurred there was no further build-up in the larval population. In fields where the wilt disease is killing off larvae in large numbers, the number parasitized by Apanteles is often less than in surrounding fields. The difference may be very noticeable. As an example, on September 3, 1941, in one field where the disease was prevalent only 16 per cent of the small larvae were parasitized, whereas in the surrounding area the amount of parasitism was 82 per cent or higher. The reason for this condition is not known, and one can only speculate concerning the cause.

It is possible that where the wilt disease is present in epidemic proportions it kills off parasitized larvae before the parasite can complete its development. The disease may be spread by the parasite. It may be that the causal organism is carried on the ovipositor. If this is the case the parasite would certainly be working against itself.

In fields where the wilt disease is present but not abundant, Apanteles is apparently not very much affected. In such fields it is not uncommon to find nearly all the small larvae parasitized. Where this condition exists it is possible that the two natural factors work independently in reducing the numbers of butterfly larvae—the wilt disease killing the larger larvae, and the parasites, the smaller. If this is the case the danger of Apanteles spreading the disease on its ovipositor is not very great, for the investigation indicates that it parasitizes only the first three instars of its host. If the larger larvae are not attacked there will be little danger of the parasite ovipositor becoming contaminated. Also, where the disease is not present in epidemic proportions the danger of the early instar alfalfa butterfly larvae contracting the disease is greatly reduced, and the chances of Apanteles becoming contaminated would thus be minimized.

DISCUSSION

This investigation has shown that there are a number of factors which influence the abundance of the alfalfa butterfly. Beyond a doubt there are many besides those studied that have a bearing upon the alfalfa butterfly population. Before control measures are instituted against the pest, the status of the biological and physical factors should be adequately known. Such knowledge as reported here should certainly be used in planning control of this serious alfalfa pest. The investigation has shown that in the summer there are three more or less definite broods. These broods have occurred in each of the four years that this study has been in progress and this natural phenomenon can be utilized in controlling the pest. If fields are closely observed, cutting might be planned so that the alfalfa would be in stubble during the periods of rapid build-up of larval populations, and would be making growth when the pest population is small.

All observations would indicate that the amount of damage done by later broods is linked with the first summer brood. If the parasitism is low at the time of the first summer brood and other conditions are favorable, a relatively large adult population will develop with few parasites to prey on it, and there is every likelihood that destructive populations will occur later in the summer. It seems, therefore, that everything possible should be done to restrict the size of the first brood. The alfalfa crop should be as carefully watched as any other crop and cut immediately as soon as mature. During the 1941 season, at this critical period, alfalfa fields were not irrigated in certain localities so that the water could be made available for the irrigation of beans. Because of this, the alfalfa grew slowly and in some fields as much as 7 weeks passed before it could be cut. In such fields, where the environmental resistance to the butterfly was low, extremely large populations of the butterfly larvae completed their development. Had these fields received proper care, it is likely that the damage caused by later infestations would have been considerably reduced.

Climate certainly plays an important role in limiting damage by the alfalfa butterfly. In the coastal regions this insect has never been observed as a pest and serious damage in California has been confined to the warmer interior valleys. The pest has been very destructive in the Sacramento, San Joaquin, Antelope, and Imperial valleys. The exact way in which climate affects the alfalfa butterfly is not known. It is possible that it prefers a warm climate and finds that of the coastal regions too cool for best development. The developmental period may be extended to a point where cutting of the crop frequently occurs before growth of the butterfly is complete. Whatever may be the cause, the observations reported here indicate that the pest will not be destructive in the coastal regions and that climate is very important in limiting damage. It is probably a very complex relationship which not only involves the growth rate of the alfalfa but also the development of the alfalfa butterfly and its parasites. In 1942 a relatively small first brood of alfalfa butterflies occurred in the northwest portion of the San Joaquin Valley when the weather conditions in that area approached that of a more coastal climate.

In this same area it has been shown that *Apanteles* has served as a very important natural enemy of the alfalfa butterfly. This parasite is so important that every effort should be made to protect it. Chemical control of the alfalfa butterfly should not be attempted until it has been determined for a certainty that *Apanteles* will not check the infestation. Insecticides should not be used indiscriminately. Under no conditions should a contact insecticide be used, unless it is very definitely known that it will kill the alfalfa butterfly larvae for which it is intended. Most contact poisons such as pyrethrum, nicotine, or rotenone are almost certain to be harmful to adult *Apanteles*; and if the parasite is killed, but the butterfly escapes, a serious infestation might result. Certainly such materials should not be used until their effect on the parasite is better understood.

It has been shown that the wilt disease is very likely to wipe out alfalfa butterfly larval populations when they become large. For this reason, if an insecticide is applied and a heavy mortality occurs, a careful check should be made to determine whether it was the insecticide or the wilt that killed the larvae. Before any insecticide is used, it should be investigated as to its interrelation with the wilt disease and parasites. An effective, suitable insecticide may be needed in some cases. If one is found, and used only where the alfalfa butterfly larva population breaks away from natural control, a suitable solution will have been found to a perplexing problem.

SUMMARY

The alfalfa butterfly, *Colias eurytheme* Boisduval, is active during most of the year. It is not until June, however, that there is any noticeable increase in the population. The first summer brood occurs at this time and although rather small, it gives rise to the destructive broods that occur in July, the last part of August, and the first part of September.

Seasonal population trends of the larvae were determined by sweeping alfalfa fields with an insect net and recording the number collected per 100

⁸ Since this paper went to press, it has been found that sulfur is effective in controlling the alfalfa butterfly larvae. A preliminary report discussing this treatment is being published elsewhere.

sweeps. The larvae were segregated into two groups according to size. All individuals smaller than the very early fourth instar larvae were classed as small, and all the rest were placed in the large group.

Apanteles flaviconchae Riley was found to be a very important larval parasite of the alfalfa butterfly, effectively reducing plant damage. It parasitizes the first three larval instars. If first-instar larvae are parasitized, the parasite will emerge from the third-instar larvae; and if second or third instars are parasitized, the parasite will issue from fourth-instar larvae. Under field conditions nearly 100 per cent of the small alfalfa butterfly larvae may be parasitized. The degree of parasitism was determined in the field by examining larvae 5 to 11 millimeters in length. The larvae were held between the thumb and forefinger and the head pulled off with a forceps. Pressure was then applied to the larva, which would cause a parasite larva if present to be expelled from the body of the host. Where the parasite larva was well developed this procedure was not necessary as the developing larva causes the posterior end of the host to be enlarged, and a parasitized larva can be detected at a glance. Experimental results obtained during the four years that the investigation has been under way would indicate that the degree of parasitism of the broad of larvae appearing in June is very important in determining the size of later broods, especially when taken with regard to the number of large worms in this early brood. Unless a good portion of larvae are parasitized by Apanteles, very destructive caterpillar populations are likely to result. Apanteles is apparently a very effective parasite because (1) it has a shorter life cycle than its host, (2) it seems to find its host with ease, and (3) it destroys its host before it has had an opportunity to do much, if any, damage.

A wilt disease frequently comes into play where Apanteles fails to check the alfalfa butterfly larval population. Usually the disease does not give any relief until the caterpillar population has become large and considerable damage is done. Under some conditions it appears that the wilt disease may make the environment unfavorable for Apanteles. The interrelationship that exists is probably complex. Where the wilt disease is not present in epidemic proportions, Apanteles appears to be little affected by it.

It was found that the number of butterflies noted was little indication of the amount of damage that might result. If the environmental resistance is low, an almost unnoticed number of butterflies might give rise to a very destructive larval population; but if these natural checks are operating, the butterflies can be extremely abundant without giving rise to a destructive larval population.

The regions studied included the agricultural area adjacent to San Francisco Bay and the northwest portion of the San Joaquin Valley. In the former region the alfalfa butterfly has never been reported as a pest, and although parasitism by *Apanteles* is rather high, it is the authors' opinion that climate is the limiting factor in holding down the population of this insect.

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